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# Natural colonisation rates in a UK upland landscape under different conservation management approaches following sheep removal

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## Abstract

1. Natural colonisation could provide a cost-effective means to increase woodland coverage across the UK uplands. However, there is a shortage of evidence of which factors affect the success of natural colonisation, including grazing management. The species of grazer, grazing intensity and the stage of regeneration may alter the impact of grazing on the ability of trees to colonise an area.
2. In this study, we quantify the effect of removing sheep from an area in the Yorkshire Dales National Park, England, and explore whether cattle or ungrazed management alters tree colonisation rates. We also tested other environmental factors such as distance from woodland, elevation and soil geology to understand the other constraints on natural colonisation. Naturally colonised trees were recorded within 60 plots at Ingleborough National Nature Reserve and surrounding Yorkshire Wildlife Trust reserves. A series of generalised linear models, with a negative binomial distribution, were created to understand the effects that years since removal of sheep, current management, elevation, distance from woodland and soil geology had on the number of naturally colonising trees.
3. The number of naturally colonising trees per hectare was 16% higher each year after sheep removal, with both cattle and ungrazed management being equally effective in promoting natural colonisation. Natural colonisation decreased by 25% for every additional 100 m from the nearest woodland and naturally colonising trees were much more frequent on limestone soil.
4. *Practical implication*. This study shows that sheep grazing is a key limiting factor of natural colonisation in the UK uplands. Significant natural colonisation was possible on both cattle grazed and ungrazed sites and developed at a similar rate, highlighting a change in grazing animal can be as important as grazing cessation. Tree planting will still be required to restore tree cover to areas away from seed sources and improve diversity of future woodlands.

KEYWORDS
cattle grazing, ecological restoration, natural colonisation, natural regeneration, sheep grazing, UK uplands, upland grazing management, woodland creation

## 1 | INTRODUCTION

The upland areas of the UK are important for biodiversity and the ecosystem services they provide. However, current and historic upland land management has left very few areas of natural vegetation (Watts & Jump, 2022); forest clearances began in the Mesolithic and continued into recent history (Shaw & Whyte, 2013; Swales, 1987). Current management now maintains an open landscape with livestock grazing and controlled burning carried out over much of the UK uplands (Fuller, 1996).

There is currently a heightened interest in measures that could increase the number of trees in upland areas (Bradfer-Lawrence et al., 2021; Jones et al., 2023), which could help store carbon at certain sites (Burton et al., 2018; Fletcher et al., 2021), alleviate downstream flooding (Marshall et al., 2014; Murphy et al., 2021; Monger, Spracklen, et al., 2022) and increase biodiversity (Douglas et al., 2020; Warner et al., 2021). There is also enthusiasm for increasing tree cover in the uplands across a range of stakeholders (FitzGerald et al., 2021). Restoration of woodland in the UK uplands, including mountain woodland that is almost absent from the UK, would bring a range of benefits (Watts & Jump, 2022).

Woodland creation can be achieved through tree planting or natural colonisation (Murphy et al., 2021). Here, we treat natural colonisation as trees colonising new areas as opposed to natural regeneration, where trees regenerate within existing woodland or recently wooded land. Natural colonisation may have several benefits over tree planting. First, the resulting woodlands will have greater structural diversity, consist of species suited to the site and protect local genetic diversity (Peterken, 1996). The resulting mosaic of woodland, scrub and open habitats created by natural colonisation are likely beneficial to biodiversity and provide habitat for rare upland species such as black grouse, whinchat and ring ouzel (Gillings et al., 2000; Scridel et al., 2017). The high structural diversity may also reduce flood risk by slowing saturation excess overland flow, especially compared with densely planted forests with sparse ground vegetation (Bathurst et al., 2020; Monger, Bond, et al., 2022). Second, natural colonisation can be highly cost-effective compared with tree planting (O'Neill et al., 2020). Lastly, due to lower levels of soil disturbance, natural colonisation may help prevent carbon losses from soil associated with tree planting (Friggens et al., 2020; Warner et al., 2022). There is limited evidence around the net carbon balance of natural colonisation compared to planting trees (when both above and below-ground carbon storage is considered), making this a priority for future research. For these reasons, there has been increased interest in the potential use of natural colonisation in recent years to increase woodland cover (Bauld et al., 2023; Broughton et al., 2021, 2022; Gullett et al., 2023; Murphy et al., 2022; Pedersen et al., 2023).

Funding mechanisms for natural colonisation are emerging in the UK, alongside those for tree planting. For example, the recently updated England Woodland Creation Offer (EWCO) requires 100 naturally colonising trees per hectare after 10 years to be eligible for funding (Forestry Commission, 2021, 2023). Sites are eligible for natural colonisation funding if they are within 75 m of a seed source, although more evidence is required on how natural colonisation varies with distance from existing trees and woodlands (Bauld et al., 2023).

There are several factors limiting natural colonisation by trees in upland areas of the UK. First, due to historic woodland loss, many sites may be too far from existing woodland to allow natural colonisation. Many species have limited dispersal, for example, Murphy et al. (2022) found no colonisation of oak beyond 75 m from woodland, the majority occurring within 20 m. Spracklen et al. (2013) found birch colonisation up to 100 m from mature birch trees. In temperate agricultural landscapes, Bauld et al. (2023) found natural colonisation within 105 m, 95% CI (70 m, 174 m) of existing forests and trees over 19 years. Even for species that are dispersed by birds such as hawthorn, birds often fly onto other areas of woodland or trees and so natural colonisation away from trees is rare (Carlo et al., 2013).

Second, high levels of grazing by both sheep and deer across much of the uplands mean sites that do have a seed source also struggle to establish naturally regenerating or colonising trees (Bunce et al., 2014; Kinnaird, 1974; Murphy et al., 2022). The number of sheep in the UK has increased over the last century. In Britain, sheep numbers more than doubled, from 19.7 million to 41.2 million, between 1950 and 1990 (Fuller & Gough, 1999). In northern England specifically, sheep numbers increased by a factor of three to five between 1900 and 2000 (Dallimer et al., 2009; Davies et al., 2022). In recent years, sheep numbers have started to fall, and in 2023, there were 31.8 million; however, that is still higher than the number in the early 20th century (DEFRA, 2023). There has also been a rise in the numbers of deer, particularly in Scotland, where numbers of red deer have increased by a similar magnitude to sheep since the 1960s (Clutton-Brock et al., 2004). There has also been a shift towards using only sheep as opposed to the mixed grazing regimes with cattle, horses and goats used in the past (Sydes & Miller, 1988). Effective grazing management is therefore one of the key management strategies for encouraging natural colonisation.

Despite it being well known that grazing has substantial impacts on vegetation in the UK uplands (Marrs et al., 2020), the effect it has on rates of natural colonisation is still not well-understood. Much of the previous research focusses on tree regeneration within existing woodland (Harmer et al., 2005; Hester et al., 1996; Humphrey & Swaine, 1997; Spracklen et al., 2013) and not on colonisation of open areas (Bobiec et al., 2018). Recent studies on natural colonisation outside of woodlands have started to address this and have shown that grazing by sheep and deer can significantly reduce the density of naturally colonising trees (Gullett et al., 2023; Murphy et al., 2022). However, the impact of grazing is complex and will depend on the species of grazing animal, grazing intensity, history of the site and stage of regeneration. At recruitment, grazing is likely to be beneficial by removing more competitive grass species and disturbing the soil to create regeneration niches (Broome et al., 2017; Morrison et al., 2019; Murphy et al., 2022; Pakeman et al., 2019; Vera, 2000). However, once the saplings have become established, they are likely to benefit from the removal or significant reduction of grazers to reduce browsing. The survival of saplings will be much lower in the presence of livestock and likely will not survive in the medium term (Murphy et al., 2022). Other factors can also further complicate this relationship between livestock grazing and sapling survival. For example, several studies have shown that a reduction in sheep numbers leads to an increase in the numbers of deer (DeGabriel et al., 2011) and voles (Evans et al., 2006; Harmer, 1995; Pigott, 1985), which could also restrict natural colonisation.

This study aimed to understand how differing grazing managements of sheep, cattle and no grazing affect natural colonisation density, at a limestone dominated upland site in the UK. We explored the timescales over which natural colonisation occurs after sheep are removed from a site and replaced with cattle or no grazing. We also investigated the effects of a range of environmental factors such as distance to woodland, elevation and soil type. We used this data to make predictions as to where natural colonisation may occur, over what timescale and at what density. This evidence will help inform future conservation strategies at similar sites across the UK uplands.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

The study site was Ingleborough National Nature Reserve (NNR) and surrounding Yorkshire Wildlife Trust reserves in the Yorkshire Dales National Park, England (54.18° N, 2.36° E). Like many upland areas in the UK, sheep grazing is the predominant land use. At Ingleborough, this has resulted in an open landscape dominated by grassland, with acid grassland covering the higher slopes and a mixture of calcareous grassland, interspersed by exposed limestone and improved grassland on the lower areas. UKCEH data shows that in 2021, woodland only covers 2.57% of the Ingleborough NNR (Marston et al., 2022). However, pollen cores from Ingleborough indicate the presence of extensive areas of woodland before clearance began at the end of the Mesolithic (Swales, 1987).

There has long been a history of conservation in the area. Over the last several decades, parcels of land have been changed from sheep grazing to cattle grazing or no grazing, with the main focus on restoring ground flora. However, it has also provided the opportunity to study the success of natural colonisation of trees over time under different conservation management strategies. Roe deer are found in the area and deer management only started in a meaningful way in 2021 at Ingleborough NNR, therefore most of the natural colonisation took place without deer management.

### 2.2 | Data collection

Natural colonisation data were recorded at 60 locations across Ingleborough NNR, nearby Yorkshire Wildlife Trust Reserves and adjacent land, covering a total area of 1195 hectares. Monitoring locations were selected to ensure that all habitats across the site were covered, with the precise plot locations selected at random. The 48 locations on the NNR were at established Natural England long-term monitoring sites. The 12 remaining plots were spread over 8 fields adjacent to the NNR. The locations of these plots were randomly selected (Random Points Inside Polygons tool in QGIS), with 1–2 plots in each field depending on its area (QGIS Development Team, 2022).

Each of the locations was grazed by sheep or had been previously, and had no or very few trees before the sheep were removed. The points were marked with a fenomarker, which acted as the centre of a circular plot of 15 m radius. Each of these plots was visited in September 2022, and all naturally colonised trees within them were recorded, including species and height (trees above 2 m height were recorded as >2 m). No licence or permits were required to carry out this fieldwork.

### 2.3 | Data analysis

There were 28 plots in areas currently grazed by cattle, 18 by sheep and 14 ungrazed. Several sites were grazed by both cattle and sheep; however, this was short-term grazing by cattle on areas predominantly grazed by sheep, these sites were therefore assigned as sheep grazed. A variable was created for the number of years since the removal of sheep on that site, 0 if sheep grazing remains (YEARS_SINCE_SHEEP). The mean number of years since the removal of sheep for cattle grazed plots was 11.14 years and the ungrazed plots 23.36 years. A second variable was created for the current management of the grazing of a plot (MANAGEMENT).

Grazing intensities of approximately 0.2 cattle per hectare per year are used for restoration management, and areas grazed by sheep having approximately one sheep per hectare per year. However, if five sheep were considered to be equivalent to one cow, then the calculated grazing intensity was comparable across sheep and cattle grazed areas (A. Hinde, personal communication, 17 March 2023). This means that any effect of changing sheep to cattle was due to the grazing animal used rather than a change in intensity. Natural colonisation is reported as the density of trees per hectare.

The distance from the centre of the plot to the nearest current woodland (DIST_WOOD) was calculated using the UKCEH Land Cover Map 2021 land parcels data set (Marston et al., 2022). The mean distance to woodland of the plots was 568 m, with a minimum of 0 m and a maximum of 1949 m. The plots at a distance of 0 m from the woodland were those that had been ungrazed for 45 years. It was not a woodland 45 years ago, but did have a few scattered trees, so there would have been a nearby seed source.

Several other variables that could possibly affect natural colonisation were also considered. The mean elevation (ELEVATION) across the plots was 373 m with a minimum of 282 m and a maximum of 643 m. Distance from woodland and elevation were correlated, with more woodland at lower elevations, and therefore both were not included in the same model.

The underlying geology and soil are important factors (Kinnaird, 1974; Pedersen et al., 2023). Soil parent material data were taken from the British Geological Survey (Soil Parent Material Model, 2018). Each plot was classified according to the definition of the parent material of the European Soil Bureaus. Of the 60 plots, 41 were classified as limestone, 8 as glacial till and 8 as peat, the remainder as riverine clay and floodplain sand and gravel or calcareous rocks and clastic rocks. All except one plot that contained natural colonisation was on limestone soil, meaning that the effects of all soil types could not be tested. Instead, a binary variable of whether the plot was on limestone soil was created (LIMESTONE). Current management and whether a plot was on limestone soil could also not be included in the same model since there were so few trees on soil other than limestone (Figure 1).

Analysis took place using R version 4.3.0 (R Core Team, 2023). A series of generalised linear models were built with a negative binomial distribution, due to the data being over-dispersed with many plots containing no natural colonisation, using the MASS package (Venables & Ripley, 2002). Models were created to test the effects of years since removal of sheep and current management, along with different combinations of distance from woodland, elevation and the binary limestone variable. There was not enough data to consider any interactions between variables within the models. Model selection then took place using AICc (an Akaike Information Criterion corrected for small sample sizes), with models being ranked based on how closely they fit the data and penalised for complexity (Burnham & Anderson, 2002). The model with the lowest AICc was selected for interpretation, but models within 2 AICc units were also considered. The models were also run with juniper excluded from the analysis due to concerns that a proportion had regrown from old root stock. However, the conclusions made if juniper was excluded were similar to those of inclusion, so it was retained in the analysis.

A second series of models were created to test which factors were important for the height of naturally colonising trees, to see whether browsing by cattle may be restricting growth. The four trees on sheep grazed plots were removed from the analysis as we were only interested in the growth rate after the removal of sheep. The same variables were used as for the previous set of models, except LIMESTONE, as all remaining trees were on limestone. A new variable of tree species (SPECIES) was also considered, with goat willow and eared willow combined. Tobit models were used due to trees larger than 2 m being recorded as >2 m. Model selection was performed with the previously described process using AICc.

## 3 | RESULTS

### 3.1 | Tree density

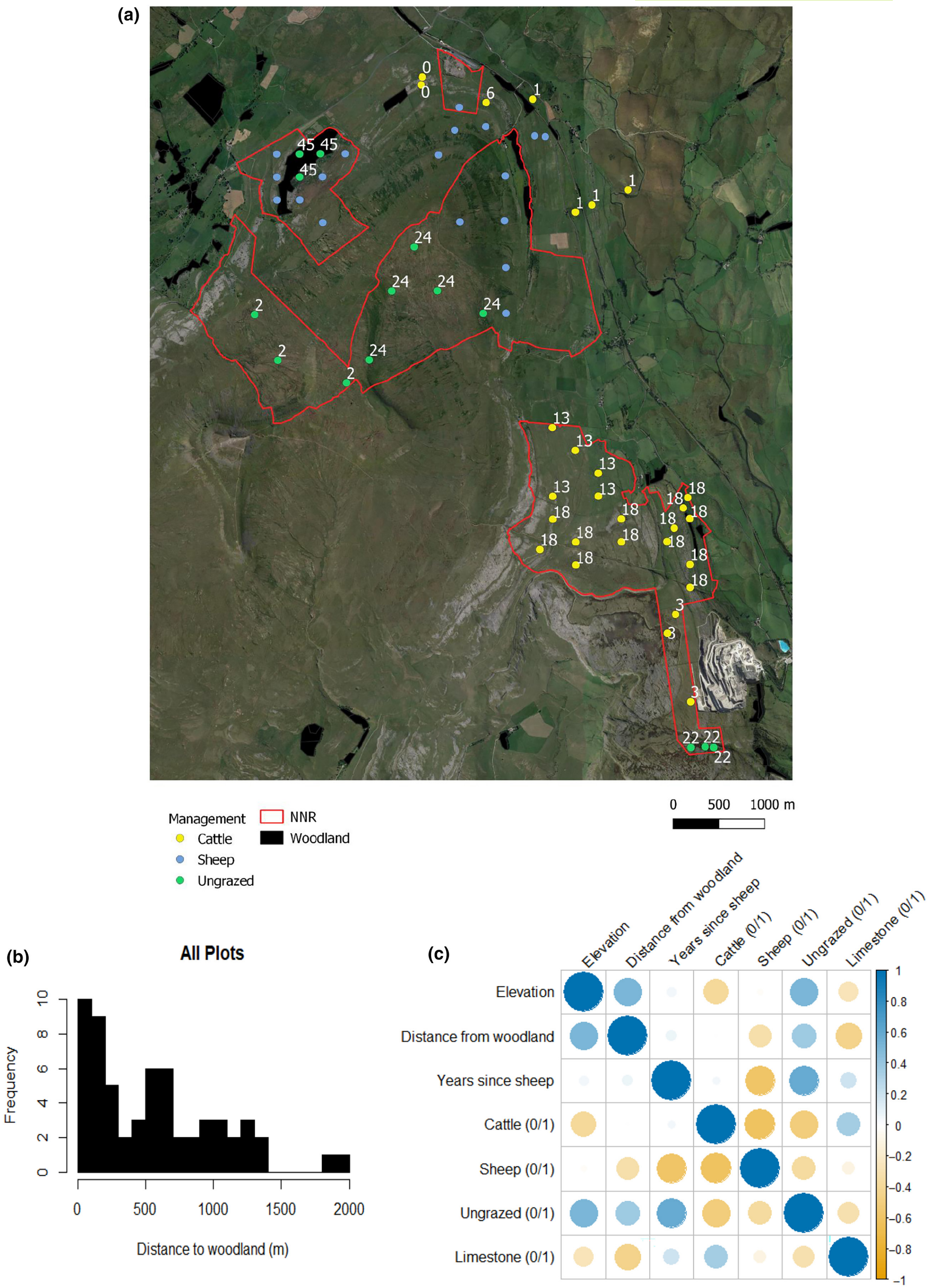
Of the 60 plots surveyed, 18 contained at least one naturally colonised tree, with a total of 509 trees in those 18 plots. In sheep-grazed plots, there was a mean density of 3.14 trees per hectare (SD 7.76). According to a Tukey's post hoc test, trees per hectare was significantly higher on both cattle grazed plots (mean = 137.43, SD 380.6) and ungrazed plots (mean = 235.5, SD 370.3), but there was no significant difference between the two (Figure 2).

The most common species found were ash, followed by hawthorn, hazel, juniper and rowan (Figure 3). All but two of the trees recorded were on limestone. Of the 50 plots that were more than 100 m from the nearest woodland edge, 9 contained at least one tree that had naturally colonised. Within those 9 plots, there were 204 trees recorded. The furthest distance from woodland was 1358 m in a plot that had four hawthorn trees.

After model selection (Table 1), the important variables for natural colonisation per plot were the years since sheep removal, the distance from nearest woodland and whether the plot was on limestone soil or not. The number of years since sheep had been removed from an area had a positive effect on natural colonisation within a plot, with the number of tree stems increasing by 16% each year since removal of sheep (rate ratio, 1.16; 95% CI 1.09 to 1.22; $p < 0.001$). Plots that were further from existing woodland had less natural colonisation, with a decrease of 25% per 100 m from woodland (rate ratio, 0.75; 95% CI 0.63 to 0.90; $p = 0.002$). The plots that had limestone as their soil parent material had significantly more natural colonisation (rate ratio, 8.48; 95% CI 1.04 to 68.82; $p = 0.045$). The confidence intervals on this effect are large, due to the lack of trees recorded on non-limestone soils (Figure 4).

Whether a site had switched to either cattle or no grazing after removal of sheep, was not found to be an important factor influencing the density of naturally colonising trees at a site. The

FIGURE 1 Figure to display the study design. (a) A map of the locations of the 60 study plots colour coordinated by grazing management (cattle = yellow, sheep = blue, ungrazed = green). Cattle and ungrazed plots are also labelled with the number of years since sheep were removed from the site. Areas of woodland, used to represent the potential seed source are black and Ingleborough National Nature Reserve is outlined in red. (b) The frequency distribution of all plots relative to their distance to woodland. (c) A correlation matrix, using Pearson's correlation coefficient, between all variables used in the study. Positive correlations are shown in blue and negative in yellow, with the shade and size of the circle being the strength of correlation between variables. Management was split into binary variables for cattle, sheep and ungrazed.


(a)
Management
Cattle
Sheep
Ungrazed
NNR
Woodland
0 500 1000 m
(b)
All Plots
Frequency
0 2 4 6 8 10
0 500 1000 1500 2000
Distance to woodland (m)
(c)
Elevation
Distance from woodland
Years since sheep
Cattle (0/1)
Sheep (0/1)
Ungrazed (0/1)
Limestone (0/1)
1 0.8 0.6 0.4 0.2 0 −0.2 −0.4 −0.6 −0.8 −1

model containing the current management, years since sheep and distance to woodland variables was outperformed by 3.01 AICc units compared to the selected model (Table 1). The output of the model shows no significant difference between cattle grazed and ungrazed sites once variables of the number of years since sheep had been removed from a site and its distance to woodland had been accounted for. The effect of elevation was also not selected for the final model.

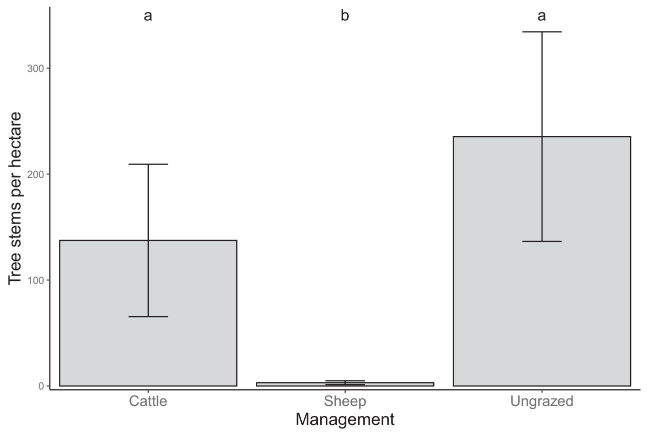



FIGURE 2 Mean trees per hectare from natural colonisation, with standard error bars, in cattle, sheep and ungrazed plots. A linear model with a negative binomial distribution was used to investigate whether there was a significant difference in tree density between grazing management. The letters indicate significance from a post hoc Tukey test, if letters are the same this indicates no significant difference.

The model predictions show that on limestone soil the requirements of 100 trees per hectare after 10 years of the EWCO could be achieved at Ingleborough NNR at a distance of 113 m, 95% CI [0 m, 383 m], from existing woodland (Figure 5). The rate of natural colonisation on other soil types on the site, such as peat and glacial till, would be lower and therefore predicted not to be eligible for funding.

We predict that in a scenario where all sheep had been removed from all sites at Ingleborough NNR simultaneously, 15.64%, 95% CI [2.57%, 35.80%], would be covered in woodland (here defined as areas with ≥1000 tree stems per hectare) through the resulting natural colonisation after 30 years. After 40 years, the woodland would have expanded further to 37.76%, 95% CI [11.49%, 88.08%]. This is a large increase from 2.57%, which is currently woodland. However, low-density woodland would extend much further and areas with at least 100 trees per hectare would cover 7.21% after 10 years, 95% CI [2.57%, 19.81%], 28.32% after 20 years, 95% CI [15.67%, 56.04%], 52.62% after 30 years, 95% CI [40.15%, 79.18%] and 71.52% after 40 years CI [42.01%, 100.00%] (Figure 6).

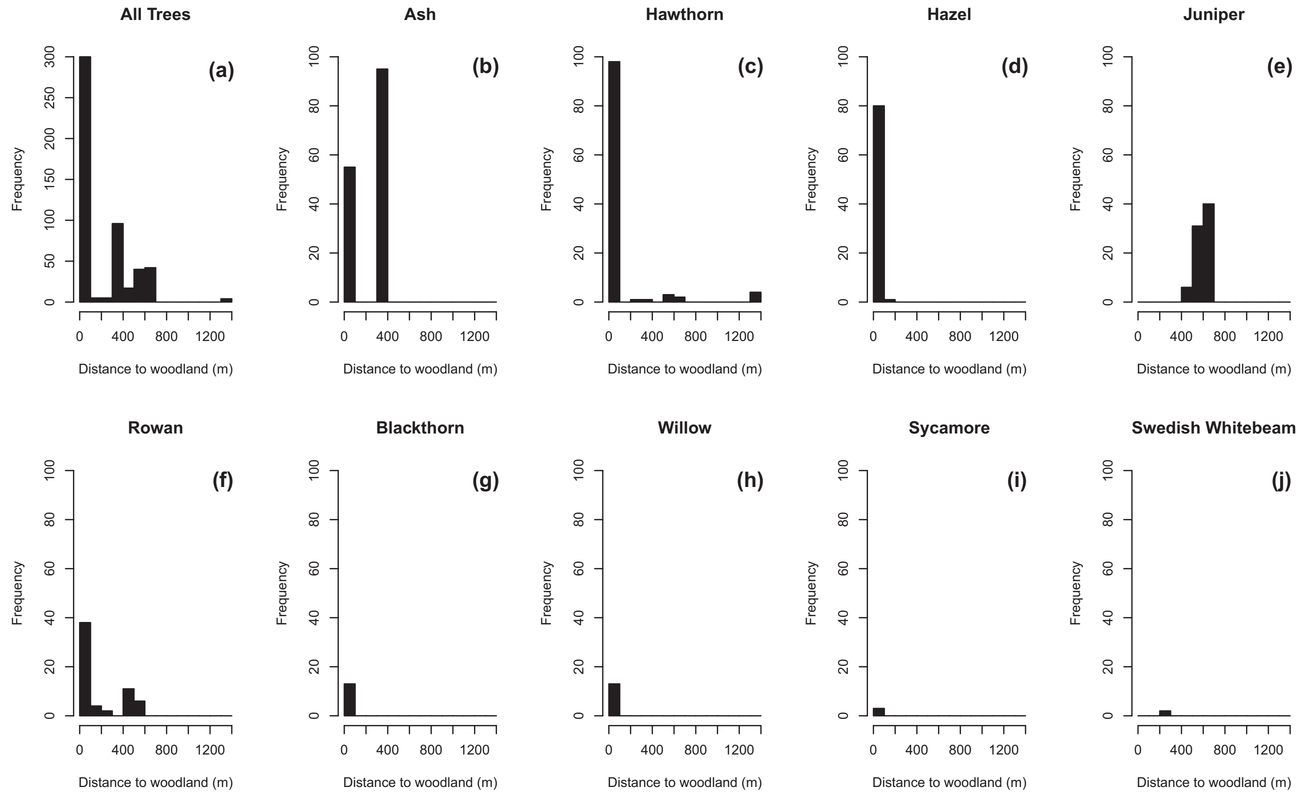



FIGURE 3 Histograms of the frequencies of trees in plots and their distance away from woodland, at intervals of 100 m. Plot (a) shows the frequency of distances to woodland of individual trees up to a distance of 1400 m. Plots (b–j) are then the frequency of individual trees of each species recorded in this study, in descending order of abundance within the surveys. Plots (b–j) share the same scale to allow easy comparison between.

### 3.2 | Tree height

Model selection showed that the important variables in determining tree height were tree species and years since sheep removal. The number of years since sheep removal had a positive effect on the height of naturally colonising trees ($\beta = 0.043$, $p < 0.001$); the mean height of a naturally colonising tree increased by 4.3 cm, 95% CI [3.7 cm, 4.9 cm] per year after sheep removal. A model containing additional variables of current management and distance to woodland was only outperformed by 0.1 AICc units. That model suggests that the height of naturally colonising trees is greater within ungrazed areas ($\beta = 0.318$, $p = 0.069$) than cattle grazed areas and closer to woodland edges ($\beta = 0.0002$, $p = 0.157$). However, both of these effects were insignificant.

**TABLE 1** Models tested to investigate the possible limiting factors on natural colonisation per plot. The number of parameters they have (*K*) and Log likelihood (logLik) of each model is displayed along with the ΔAICc.

| Model | *K* | LogLik | ΔAICc |
|---|---|---|---|
| YEARS SINCE SHEEP+DIST. WOOD+LIMESTONE | 5 | −95.81 | 0.00 |
| YEARS SINCE SHEEP+DIST.WOOD | 4 | −97.63 | 1.26 |
| YEARS SINCE SHEEP+MANAGEMENT+DIST. WOOD | 6 | −96.08 | 3.01 |
| YEARS SINCE SHEEP+ALTITUDE | 4 | −98.84 | 3.68 |
| YEARS SINCE SHEEP+ALTITUDE+LIMESTONE | 5 | −97.77 | 3.91 |
| YEARS SINCE SHEEP+LIMESTONE | 4 | −99.47 | 4.93 |
| YEARS SINCE SHEEP+MANAGEMENT+ALTITUDE | 6 | −98.07 | 6.98 |
| YEARS SINCE SHEEP | 3 | −102.04 | 7.77 |
| YEARS SINCE SHEEP+MANAGAMENT | 5 | −100.75 | 9.87 |
| NULL MODEL | 2 | −108.01 | 17.51 |

## 4 | DISCUSSION

Our results are a clear demonstration that removing sheep grazing will benefit natural colonisation in upland limestone landscapes, even in areas that have a very limited overall woodland cover. This would provide a cost-effective strategy to increase woodland cover in such areas (O'Neill et al., 2020). The woodland created would be highly variable and densities of more than 1000 trees per hectare would be predicted at 91 m, 95% CI [0 m, 528 m], from existing woodland 30 years after removal of sheep grazing. We show that sheep grazing, distance to woodland and soil type are all important limiting factors to natural colonisation in the UK uplands.

Our results show that removing sheep from an upland limestone landscape and leaving it ungrazed or grazing with cattle will lead to increased natural colonisation of trees over time. The benefit of complete removal of livestock from a site for natural colonisation is likely explained by the reduction in browsing pressure. A study by Murphy et al. (2022) showed increased browsing damage on oak saplings on areas grazed by sheep, compared with areas from which they were excluded, resulting in stunted growth and a very low survival rate beyond 7 years. This browsing damage and low survival rate led to a similar difference in the density of naturally colonising

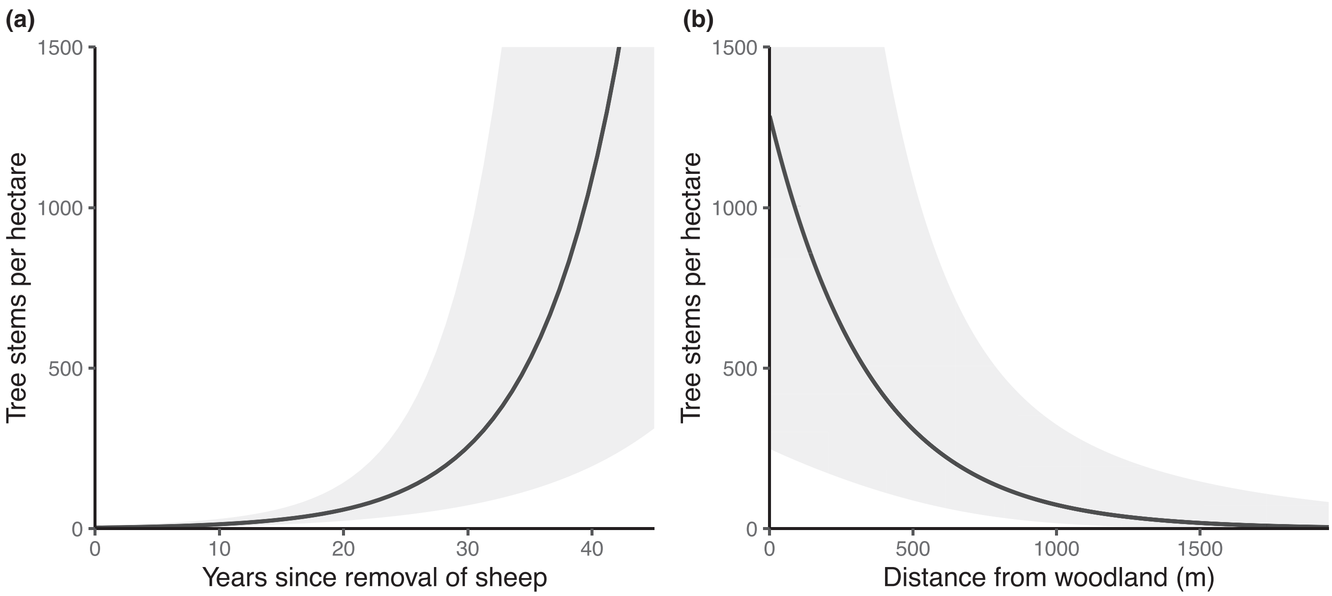



**FIGURE 4** Model predictions, of tree stems per hectare against (a) years since the removal of sheep and (b) distance from the edge of nearest woodland. Mean (solid line) and with 95% confidence intervals (grey shading) are shown. Model predictions for natural colonisation at different years since removal of sheep were at the mean of other variables within the model (Distance from woodland = 562 m, Limestone = 0.61). Predictions for natural colonisation at different distances from nearest woodland were at the mean for limestone and at 30 years since the removal of sheep.

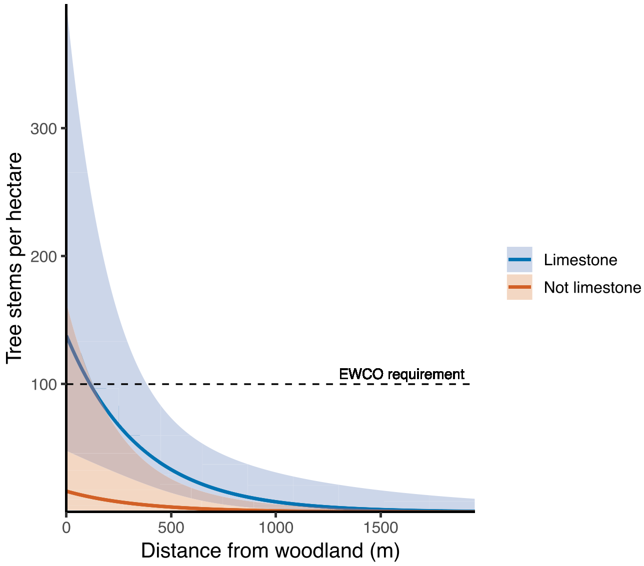



FIGURE 5 Model predictions of the number of tree stems per hectare against distance from the edge of nearest woodland, for both areas on limestone soil-parent material and areas that are not. Predicted mean (solid line) and 95% confidence intervals (shading) are shown. Predictions were calculated for 10 years since removal of sheep to allow comparison to England Woodland Creation Offer (EWCO) natural colonisation targets of 100 stems per hectare after 10 years (black dashed line).

trees between sheep grazed and ungrazed areas as was observed within our study. More research to understand whether natural colonisation would be possible under even lower stocking densities of sheep would be useful. However, the density of one sheep per hectare in our study is still lower than in many parts of the UK uplands, with densities often exceeding two sheep per hectare (Thompson et al., 1995).

Importantly, our study also highlights natural colonisation of trees can be achieved whilst shifting from sheep to cattle grazing, even if grazing intensity is consistent. Several factors may lead to increased natural colonisation with cattle grazing, first, the less selective grazing behaviour of cattle means they may not preferentially graze seedlings like sheep do (Cuchillo-Hilario et al., 2018; Grant et al., 1985). Sheep are known to target plants of higher nutritional value, while cattle will graze areas with higher overall plant biomass (Marrs et al., 2020; Török et al., 2014). Sheep have the dental anatomy to be able to achieve this selectivity by using their incisors to bite single plants, whereas cattle wrap their tongue around plants (Rook et al., 2004). A second potential reason for cattle grazing leading to increased natural colonisation may be due to their hooves creating greater ground disturbance, breaking up vegetation and creating areas of bare soil (Betteridge et al., 1999). This disturbed ground may provide regeneration niches, giving tree seedlings an increased chance of establishment. Lastly, the species composition of

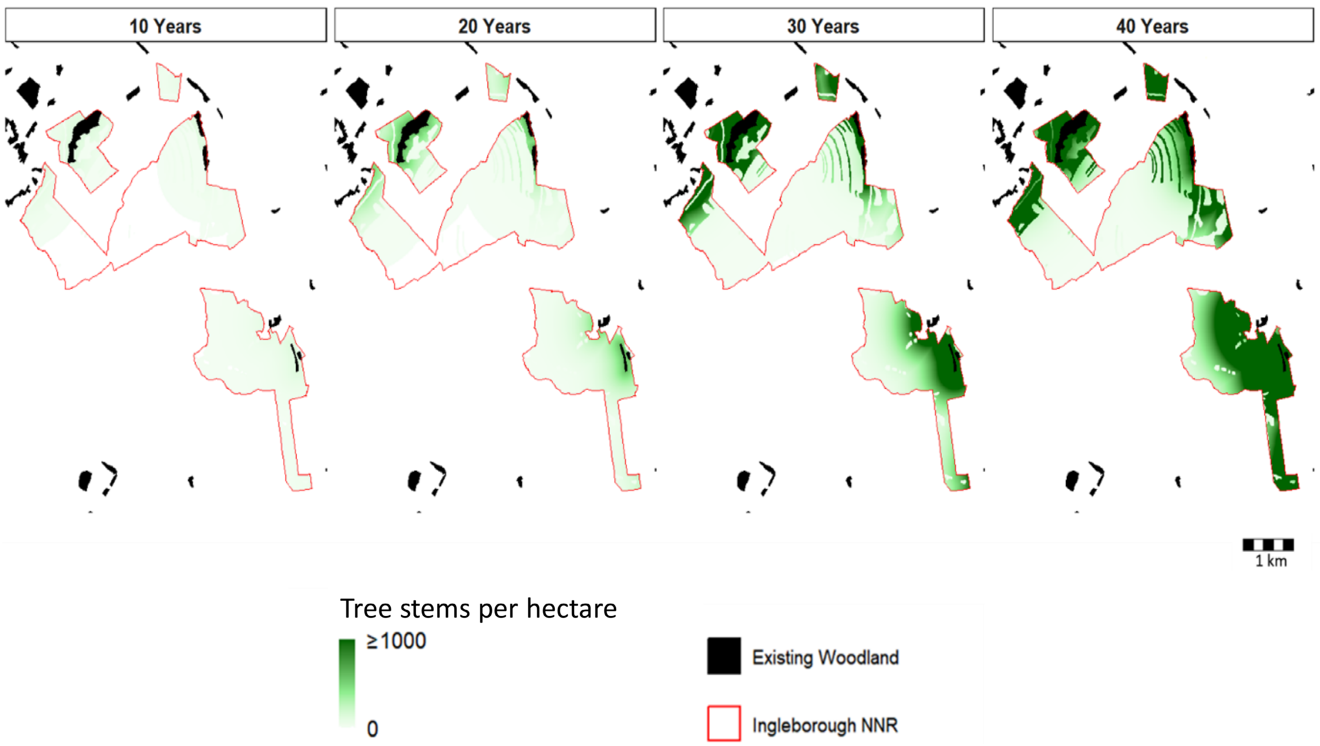



FIGURE 6 Mapped model predictions of tree stems per hectare at Ingleborough National Nature Reserve (red line) at 10, 20, 30 and 40 years since removal of sheep from the area. Existing woodland is also shown (black). Predictions of densities of natural colonisation over 1000 per hectare are shown as 1000 per hectare.

the sward is also likely to be different under cattle and sheep grazing, with a higher proportion of forbs in cattle-grazed areas (Tóth et al., 2018). This difference in composition could also influence the rate of natural colonisation if tree seedlings face less competition from the surrounding vegetation in cattle-grazed areas.

It is also important to consider that changing the grazing on a site will affect more than just the rate of natural colonisation and the effect it may have on biodiversity is complex. For example, previous research on limestone soil at Ingleborough NNR suggests that removing sheep and leaving a site ungrazed will reduce diversity of ground flora but switching to cattle would maintain this diversity (Lyons et al., 2017). This suggests that cattle grazing could be a better management option than leaving sites ungrazed. However, ungrazed management does result in greater structural complexity of vegetation, which is also important for biodiversity (Lyons et al., 2018). Different species assemblages of plants, spiders and ground beetles are associated with different grazing management, this suggests that at a landscape scale having different types of grazing management would be optimal for biodiversity (Lyons et al., 2017, 2018, 2022).

In addition to the effects that changing grazing management can have on biodiversity, other previous research at Ingleborough NNR has highlighted that it can also affect carbon storage. Edgar (2019) found higher soil carbon in areas on limestone soil where sheep grazing had switched to cattle or ungrazed at least 10 years ago, than areas where sheep remained. Although Medina-Roldán et al. (2012) did not find a change in soil carbon after 7 years between a sheep-grazed area and an ungrazed area on peat soil, there was an increase in above-ground biomass and a slower rate of soil decomposition.

Our results show a clear positive effect of limestone soil parent material on natural colonisation. However, the strength of this effect was uncertain due to the lack of colonisation on other soil types such as peat and glacial till. This result, however, still highlights that soil type is an important consideration for whether a site is suitable for natural colonisation, as has also been shown in other studies (Kinnaird, 1974; Pedersen et al., 2023). Natural colonisation may have been higher on limestone soil for several reasons. First, limestone pavement may provide regeneration niches between rocks where competition with other plants is reduced. Second, differences in soil moisture and pH may also be important, particularly for the colonisation of certain species of tree. The unique limestone pavements of the area may also help explain why ungrazed treatments experienced as much natural colonisation as cattle grazed sites. Ungrazed areas on limestone may not be limited by a lack of regeneration niches due to competition from other plants as might be expected on other soil types (Broome et al., 2017; Morrison et al., 2019; Murphy et al., 2022; Pakeman et al., 2019; Vera, 2000). However, it is also possible that limestone pavement contributes to the success of natural colonisation in cattle-grazed areas, as cattle are less likely to access the pavement than sheep. It is therefore possible that the effect grazing by different species has on natural colonisation is dependent on soil type and landscape features. More research is needed to understand how these site-specific factors can interact with the effect of grazing.

We also find that natural colonisation is clustered around existing woodland and is sparse away from seed sources. Therefore, the success of natural colonisation will depend on the frequency and distribution of seed sources in the landscape. The results, however, also show several apparent examples of long-distance dispersal, up to 1358 m, by trees. These distances are much greater than would be expected based on the 75 m maximum from Murphy et al. (2022) and 100 m maximum in Spracklen et al. (2013). Although some of these trees had seed sources closer than the nearest woodland identified (further elaboration will be provided subsequently), many had no obvious seed source within 100 m and so suggest that long-distance colonisation is possible by certain species of trees such as hawthorn.

New funding schemes are supporting woodland creation through natural colonisation. The EWCO requires the site to be within 75 m of a seed source and have achieved a density of 100 trees per hectare after 10 years (Forestry Commission, 2021). Our results show that the target density could be achieved after 10 years up to a distance of 113 m, 95% CI [0 m, 383 m], from existing woodland. Our predictions highlight that funding through the EWCO would be available for natural colonisation at Ingleborough NNR and may be appropriate for other similar limestone dominated upland landscapes in England.

While natural colonisation is clearly possible in the uplands and there is funding to support it, our results also highlight the importance of tree planting to increase tree cover away from seed sources. This conclusion is shared by recent studies in temperate agriculturally dominated landscapes (Bauld et al., 2023; Broughton et al., 2022) and upland acidic oak dominated landscapes (Murphy et al., 2022). Firstly, natural colonisation is biased towards species which are effective dispersers and those already in the area, meaning rare key species may be missing. For example, birch and oak are common in the Ingleborough pollen record (Swales, 1987), but they are uncommon in nearby woodlands, and neither were recorded during the surveys. Active restoration by planting these missing trees and other rare species is likely to lead to greater diversity (Keller et al., 2023). Secondly, due to natural colonisation decreasing as distance from woodland increases, some areas are simply too far from woodland to experience meaningful natural colonisation in decadal timeframes (Bauld et al., 2023; Murphy et al., 2022). Applied nucleation could be used in these areas to provide a seed source for natural colonisation in the future (Holl et al., 2020). Lastly, the progress of natural colonisation in the UK uplands is slow, even near areas of woodland, and it will take a long time for a woodland to develop. We predict an increase of just 43 cm, 95% CI [36 cm, 49 cm] in the height of the average tree every 10 years since the removal of sheep. Planting trees will likely speed up the time taken to reach a woodland, if that is the desired end goal.

The approach used here to predict natural colonisation could be useful to inform future management at sites and highlight where tree planting will be required. We predict that natural colonisation would increase the current woodland cover on Ingleborough NNR of 2.57% to 15.64% over 30 years, 95% CI [2.57%, 35.80%], if considering areas over 1000 trees per hectare as woodland. Predictions show where additional tree planting may be needed for woodland creation over these timescales (Figure 6). Despite possible future utility, the exact predicted values should be interpreted cautiously at present as they are informed by a relatively small sample of data. In particular, more data from cattle and ungrazed sites on a variety of different soil types is required. Natural colonisation surveys will continue to be carried out as part of the Wild Ingleborough project at more sites and over increased numbers of years, which should lead to increased accuracy in future predictions. Expanding data collection at a wide range of different sites, with different soil types, would also allow predictions to be made in much larger areas.

One of the main limitations of this study is the spatial resolution of our data on existing seed sources. We use the UKCEH land cover map which identifies existing areas of woodland, but excludes individual or clumps of trees outside of woodland, which may act as important seed sources. Although trees outside woodlands are rare at Ingleborough NNR, it would be beneficial to map such seed sources in future, manually or using aerial imagery, to allow more accurate prediction of natural colonisation. The relationships between natural colonisation and distance to seed source may change if seed sources outside of woodlands are included in the analysis. A measure of connectivity to seed source would likely further improve the predictions. Pedersen et al. (2023) show that the quantity of seed source at a site is important in addition to distance.

## 5 | CONCLUSIONS

We show that shifting from sheep grazing to cattle grazing or no grazing leads to natural colonisation of trees in an upland limestone landscape in England. We find similar rates of natural colonisation in both cattle grazed (0.2 cattle per hectare) and ungrazed management. Natural colonisation is concentrated around existing woodlands and declines by 25% for every 100 m distance from a seed source. Land managers can use the presence of limestone soils and the distance to seed sources to predict where natural colonisation is likely to occur. Tree planting may be required to deliver increased woodland cover in areas further from a seed source on decadal timescales.

### AUTHOR CONTRIBUTIONS

George Porton, Dominick Spracklen and Cat Scott conceived the ideas and designed methodology; Robyn Wrigley collected the data; George Porton analysed the data; George Porton led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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### CONFLICT OF INTEREST STATEMENT

There was no conflict of interest.

### PEER REVIEW

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### DATA AVAILABILITY STATEMENT

Data sets made available on Zenodo https://zenodo.org/record/8238521 (Porton et al., 2023).

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